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Population Dynamics of *Australorbis glabratus* in Puerto Rico

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This report on the population dynamics of Australorbis glabratus *in Puerto Rico is based on observations made over about two years at 50 collecting-sites in a representative range of snail habitats. In some places a marked predominance of* Tropicorbis *was noted. No continuous or seasonal propagation of* Australorbis *was apparent. Dense populations seldom prevailed for more than a few months, and in most places very low population levels occurred at irregular intervals, and colony decimations were fairly common. A variety of pressures is exerted on* Australorbis *in Puerto Rico by a multiplicity of natural factors; detailed knowledge of this snail's natural history in the field is necessary for effective bilharziasis control and for a full understanding of the regional epidemiology of this disease.*

The need for biological studies on the snail vectors of bilharziasis has been repeatedly emphasized (Olivier, 1955; McMullen & Harry, 1958). Olivier (1955) stated: "A study of snail biology set up as a continuing project in a variety of natural habitats would surely pay large dividends. Subjects to be investigated in this way should include population dynamics . . .". This paper reports on a study of the population dynamics of *Australorbis glabratus*, vector of *Schistosoma mansoni*, as it occurs in swamp, stream, river, irrigation canal, lake and farm pond habitats in Puerto Rico. Periodic intervals of observation were planned for a minimum of two years. "Continuing projects" of this type for *Australorbis* and related species in different geographical areas and for varied habitats are certainly still too few. The chief contributors to this type of study include Olivier & Barbosa (1955) on *Australorbis* in Brazil, Liétar (1956) on *Biomphalaria* in the Congo and Cridland (1957, 1958) on *Biomphalaria* in Uganda; in Puerto Rico, Pimentel & White (1959a), Rowan (1959) and H. W. Harry[4] made observations on population dynamics and factors of influence for the stream habitat, and F. F. Ferguson[4] on populations in cane-field drainage ditches.

The observations of Olivier & Barbosa (1955) were made in areas that contained water only during the wet season (April to August). A sparse population residue of *Australorbis* surviving after a dry period of seven months (April) was sufficient to propagate a thriving colony two months later. However, for the rest of the wet season, propagation was negligible. In permanent pools, reproduction was continuous but there were occasional unexplained decreases in snail numbers, even to very low levels. Cridland (1957) found that *Biomphalaria* became prevalent in a permanent body of water about two months after the onset of the rainy season (April) with peak populations between August and January, varying somewhat for different species. The occurrence of juveniles was not continuous but limited to the earlier part of the rainy season. During the dry season, the snail population dropped to a low level, even though the habitat was a permanent body of water. In a permanent stream (Cridland, 1958) the adult population was continuous throughout the year, but propagation was inconstant. The occurrence of juveniles was associated with the onset of rains. Liétar (1956) noted that in stagnant water the *Biomphalaria* were most prevalent near the end of the rainy season, while in running water propagation was associated with the dry season. In the streams of Puerto Rico studied by Pimentel & White (1959a) and by Rowan

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(1959) low populations of *Australorbis* were correlated with the rainy season (April-November) and the higher densities with the dry season. The opposite was true for the cane-field drainage systems observed by F. F. Ferguson;[1] these stagnant habitats had most snails during the rainy season, but they had their origin in associated small field drains from which they were flushed.

PROCEDURES

Snail collections in this study were made at permanently marked collecting-sites[2] at approximately 6-week intervals. There were some deviations to 3- and 12-week intervals, when the development of the data indicated that such were necessary. On each occasion 25 snail samples were taken throughout a distance of 50-100 feet (15-30 m) by means of a standard wire-mesh scoop. A sweeping movement of about three feet (or approximately 1 m) over the soil or through the vegetation was made. This procedure was standardized by Gerhardt,[3] who demonstrated that ten such sweeps yielded snails approximating the numbers in adjoining square-yard quadrates. In our investigation, sampling was randomized, but incorporated a studied attempt to gather the maximum numbers of snails. As each scoop-recovery was made, the snails were counted according to three estimated size categories: small (7 mm or less), medium (8-15 mm), and large (over 15 mm). In some instances more precise measurements of 1-mm increments were made in the laboratory. In one series of prolonged observations in the Caguitas River, the snail survey method differed as noted below. Cursory observations were recorded on conspicuous environmental conditions which might account for snail fluctuations. Prevalence of infections was checked occasionally.

RESULTS

Miranda swamp

Miranda swamp, near Trujillo Alto, comprises about a quarter of an acre (or about 1000 m²), of which about half is continually covered with open, clear water with a maximum depth of three feet (or a trifle over 90 cm). It is spring-fed; the bottom is mucky; and the margins are densely covered with grasses and reeds. Environmentally, Miranda swamp remains unchanged seasonally. A sizeable snail population was present when observations began (April 1957) but propagation was not apparent at any time, and snails collected did not exceed medium sizes (8-15 mm). A definite decline in numbers of *Australorbis* occurred soon after observations were begun and continued for about 6 months (Table 1). At a low point in the population curve,

TABLE 1
SUMMARY OF PERIODIC COLLECTIONS OF *AUSTRALORBIS* IN MIRANDA SWAMP

Month of collection	No. snails per 25 dips
1957	
April	79
May	54
July	47
August	76
September	19
November	14
December	3
1958	
January	4
March	2
April	5
June	5
July	3
August	5
October	1
November	1
1959	
January	1
February	1
March	0
June	1
September	0
1960	0
1961	0

[1] Unpublished manuscript.

[2] The collecting-sites are numbered from upstream to downstream in the tables, where applicable.

[3] Gerhardt, C. E. (1956) Unpublished summary of investigations No. 7, Technology Branch, Communicable Disease Center, Public Health Service, US Department of Health, Education, and Welfare.

TABLE 2
EVALUATIONS OF *AUSTRALORBIS* POPULATIONS IN RIO CAGUITAS [a]

Year of collection	Collecting-site:				
	1	2	3	4	5
1954	Abundant	Abundant	Abundant	Abundant	Abundant
1955	Moderate	Moderate	Moderate	Abundant	Moderate
1956	Sparse	Sparse	Moderate	Moderate	Moderate
1957	Rare	Rare	Rare	Sparse	Rare
1958	None	None	None	Rare	None
1959	Rare	Rare	Rare	Sparse	Rare
1960 [b]	None	Abundant	Abundant	Sparse	Sparse

[a] Rare = 1 snail or less per square yard; sparse = 2-5 snails per square yard; moderate = 6-20 snails per square yard; abundant = over 20 snails per square yard.

[b] During the first quarter of 1961, snails were rare or absent at all collecting-sites, reflecting conditions for the entire river.

a competitor snail, *Marisa*, appeared (January 1958). In April 1958, the latter was predominant and after June 1959 *Australorbis* was no longer collected. This situation prevailed through March 1961.

There was no apparent explanation for the decline of snails in the Miranda swamp. It was a permanent body of water, not unlike those studied by Olivier & Barbosa (1955) and Cridland (1957). The former found reproduction continuous, with occasional population declines, while Cridland found propagative activity following the onset of the rainy season. In contrast, we found a decline throughout the rainy season, undoubtedly due to some local, unrecognized influence. The absence of any repopulation for a period of 2½ years may have been linked with the appearance of *Marisa* after *Australorbis* had declined.

Rio Caguitas

Rio Caguitas, a small river in eastern Puerto Rico, was extensively populated with *Australorbis* and five collecting-sites were studied from 1954 to 1961. These sites were located in a 5-mile (8-km) low-gradient (0.5%) section, where snail colonies are seldom disrupted by rain storms, excepting severe ones. The water is generally clear and emarginated by grasses and *Caladium* (elephant-ear plant), the latter dominating. The river is grossly polluted for a distance of about half a mile (about 800 m) below the outfall of an Imhoff tank located 400 feet (about 120 m) above collecting-site 5. Population evaluations were made on a monthly basis and snail numbers were recorded as rare (one or less per square yard [1]), sparse (2 to 5), moderate (6 to 20) and abundant (over 20). *Australorbis* was abundant at all five collecting-sites when observations were started in 1954 (Table 2). Thereafter a progressive decline in numbers occurred through 1958, when snails were not recovered from four sites and were rare in the fifth. During 1959 repopulation began to occur, and in 1960 snails were abundant in two sites, sparse in two and still lacking in one. Infected snails are frequently encountered in collections from the Caguitas river.

An additional collecting-site (No. 6) was selected on the Caguitas river in 1957 (Table 3). It was located about 100 yards (or about 90 m) below collecting-site 4 of the above series, and population densities were quantitated on the basis of 25 scoop-recoveries. Initially the snail count was abundant (89 per 25 dips), although at collecting-site 4, 100 yards away, snails were recorded as sparse at that time. However, a decline in numbers occurred at collecting-site 6 during 1957; in 1958 there was a period when snails were not collectable, and the population thereafter remained at a negligible level into 1961.

The progressive decline of *A. glabratus* in the Caguitas river over a period of four years from abundance to near-eradication has no precedence

[1] 1 square yard = 0.8 m².

TABLE 3
SUMMARY OF PERIODIC COLLECTIONS OF *AUSTRALORBIS* IN RIO CAGUITAS

Month of collection	No. snails per 25 dips
1957	
April	89
May	57
July	16
August	10
October	3
November	6
1958	
February	13
March	3
May	3
July	0
August	0
November	0
1959	
January	0
March	1
June	1
September	0
1960	
March	0
1961	
January	0

in the literature. Attention was focused on the massive invasion of a foreign snail, *Tarebia granifera mauiensis*, as a possible suppressive influence. On one occasion in 1958 a series of 10 dips yielded numbers ranging from 314 to 917 per dip. However, reappearance of the vector snail now imposes doubt that *Tarebia* caused the decline in *Australorbis*.

Correlated with population failure on the part of *Australorbis* was a decrease in the occurrence of bilharziasis in the children of adjacent communities. The prevalence rate was 17% in 1954 and 6% in 1957, at which level it persisted through 1959.

Rio Aibonito

Rio Aibonito (a stream) was observed in August 1958 to have a very dense population of uniformly large (20 mm) *Australorbis* with a high rate of infection. In December 1958 this stream was included for " periodic " study after several collections for positive snails. About a quarter of a mile (or 400 m) above this snail concentration, the activated sludge outfall from the sewage facilities of Aibonito entered the stream. Five collecting-sites were established in the second quarter-mile sector below the point of contamination and a sixth site was selected one mile (1.6 km) further downstream. Heavy pollution was indicated by a progressive downstream change in water colour from grey to clear. Marginal and submerged vegetation was very dense, requiring severe rains to dislodge the mats of *Piaropus* (water hyacinth) and the snails.

After the surveys were started in early December 1958, a decline in snail population became apparent within two months at collecting-sites 1-5 (Table 4). This decline continued throughout the dry season until by mid-1959 snails were rare, remaining so through March 1960. Then in July 1960 a dense population again occurred, except at site 1. During the prolonged period of low population at sites 1-5 the snail colony at site 6 was relatively stable.

Initially, the infection rates were as high as 25% (sites 1-5), dropping to 10% when the periodic observations were started and lower as the snails became sparse in 1959. After repopulation in 1960, the rate was 5%.

Whereas Pimentel & White (1959a) and Rowan (1959) noted maximum propagation in high-gradient streams during the dry season (December-March) with decline during the wet season (April-November), our observations of the Aibonito stream differed. Dense populations occurred in the rainy seasons of 1958 and 1960, but not in 1959, with no propagation in the two intervening dry seasons. We believe the following factors of difference may be involved. First, the gradient of flow in the sector of the Aibonito stream studied was low (Harry & Cumbie, 1956) and the amount of vegetation was very great. These conditions would tend to protect snails from being washed out by normally heavy rains. Secondly, absence of propagation in the dry season is thought to be linked with pollution, because while the stream-flow declines, the volume of sewage would remain relatively constant. Pollution was further intensified in the dry seasons of 1959 and 1960 because of low rainfall, particularly in 1959. Low precipitation occurred throughout the 1959 rainy

TABLE 4
SUMMARY OF PERIODIC COLLECTIONS OF *AUSTRALORBIS* IN RIO AIBONITO

Month of collection	No. snails per 25 dips at collecting-site:					
	1	2	3	4	5	6
1958						
August	Abundant	Abundant	Abundant	Abundant	Abundant	Abundant
December	16	54	11	58	53	44
1959						
January	4	—[a]	4	19	12	26
February	0	—	0	9	2	8
March	1	8	0	1	1	0
May	10	1	6	2	3	38
June	7	3	6	0	2	58
July	0	0	0	3	0	38
September	3	0	11	0	0	36
October	0	0	2	2	3	—
December	3	1	0	2	0	44
1960						
January	2	1	0	3	0	43
February	0	0	0	1	0	22
March	0	0	0	1	0	30
July	0	40	69	49	79	43
July	0	110	69	64	145	[b]
August	0	50	39	56	50	5

[a] A dash indicates that no collection was made.
[b] Molluscicide applied through the waters of a confluent stream.

season at Aibonito, the annual average being reduced by nearly 50% (33.6 inches, or 854 mm, as compared with a long-range mean of 60.0 inches, or 1524 mm). Thus the influence of pollution may have persisted throughout the year, accounting for the absence of snails during the rainy season of 1959. The relatively stable colony at collecting-site 6, where pollution was greatly reduced by distance, is consistent with this explanation. It is further inferred that, whereas heavy pollution in low-gradient streams is corrected for snail habitation only by the freshening rains during the wet season, rapidly flowing water of high-gradient streams may preclude the effect of pollution at all times. A relationship of freshening rains to propagation of planorbids also appears to apply to the findings of Cridland (1957), Liétar (1956), Ferguson [1] and possibly Olivier & Barbosa (1955).

Lajas irrigation system

The Lajas irrigation system in southwestern Puerto Rico will ultimately supply 26 000 acres (or about 10 500 ha). Completed portions have been in use since August 1955. The distribution system is cement-lined throughout, except for the drainage canals. The flow-rate is rapid in the primary canal and consequently vegetation is sparse except in terminal sectors, where it sometimes accumulates with silt. The secondary delivery channels are also cement-lined, well graded and frequently dried. Six new, interconnected lake-reservoirs supplying the

[1] Unpublished manuscript.

TABLE 5
SUMMARY OF PERIODIC COLLECTIONS OF *TROPICORBIS* AND *AUSTRALORBIS* IN LAJAS IRRIGATION CANAL

Month of collection	No. snails per 25 dips at collecting-sites:		
	1-3	4-6	7 & 8
1957			
November	0	0	0
1958			
January	0	0	0
February	0	0	0
April	0	5 [a]	0
June	0	0	0
August	0	0	0
October	0	0	72
December	0	0	0
1959			
January	0	3	35
March	0	2	24
April	0	0	0
July	0	1	1
1960			
January	0	0	0

[a] *Australorbis* in water-exit basin; all other entries are *Tropicorbis*.

Lajas system have steep slopes with wave action, and vegetation has not yet accumulated.

Planorbid snails have been infrequently encountered in the main canal and chiefly limited to the lower sectors, where vegetation and silt collect (Table 5). Recorded specimens were identified as *Tropicorbis*, but on one occasion a few large shells typical of *Australorbis* were obtained in the upper portion of the canal, and at the same time and place a few living specimens were found in a water-exit basin, indicating that *Australorbis* had actually gotten into the canal but failed to propagate. Planorbids have rarely been collected in the reservoirs. Since the Lajas area is naturally arid, *Australorbis* was confined originally to the overflow of windmill pumps, a few farm ponds and permanent impoundments along commonly dried streams.

It appears that planorbids, especially *Australorbis*, will not thrive in most sections of the cement-lined main canal of the Lajas system, because of swift currents and good management. Secondary channels will certainly prove unfavourable because of frequent drying. The lake-reservoirs are unpredictable since findings vary in similar older impoundments. The importance of the dirt-lined drainage canals is also uncertain. Following the onset of irrigation in 1955, there has been a noticeable increase in terminal drainage seeps and permanent natural streams, which constitute potential snail habitats. By 1961, extra-canal distribution of *Australorbis* had increased in area by 50%.

Guajataca irrigation system

The Guajataca irrigation system in northwestern Puerto Rico has two parallel canals (north and south). Upstream the flow is rapid, but it declines in rate to a point that is favourable for planorbid habitation. The flow is interrupted only for brief periods of repair, because the water of one canal, in addition to being used for irrigation, serves a local hydroelectric power plant near the end of the canal, and the other canal is the sole source of water for Ramey Air Force Base. Massive growths of vegetation, particularly *Najas*, develop in the channels, in which planorbids occur abundantly at times (Table 6). Periodic manual cleaning of the canals is required at 3-month intervals.

Australorbis and *Tropicorbis* were both found in each of the two canals, primarily in unmixed colonies. These identifications were made initially by Dr Bengt Hubendick and Dr Charles S. Richards. In the south canal *Australorbis* occurred at collecting-site 4 downstream, while in the north canal it occurred further upstream at site 5. *Tropicorbis* dominated almost totally at all other collecting-sites (1, 2, 3 south; and 6, 7 north). *Australorbis* was collected at site 4 for the first four surveys only and then was not found for the rest of the study period, or one and a half years. At collecting-site 5 (north) the colony was relatively stable for a year, then snails were not collectable for two surveys but reappeared after that. Numbers of *Tropicorbis* varied greatly from one survey to the next and for the different sites, and maximum numbers did not persist from one collection to another (six weeks). Peaks of population were apparent for all colonies at about the same times in 1958 and 1959. Between these peaks snails were not collected for a period at two sites; and shortly after the 1959 peak, snails were not found at any of the sites.

Marked fluctuations and disappearances of both *Australorbis* and *Tropicorbis* could not be linked

TABLE 6
SUMMARY OF PERIODIC COLLECTIONS OF *AUSTRALORBIS* AND *TROPICORBIS* IN GUAJATACA IRRIGATION CANALS

Month of collection	No. snails per 25 dips						
	South branch collecting-sites: [a]				North branch collecting-sites: [a]		
	1 [b]	2 [b]	3 [b]	4 [c]	5 [c]	6 [b]	7 [b]
1958							
April	113	59	—[d]	189	—	142	—
May	51	22	—	21	—	427	—
July	961	276	187	23	—	151	50
August	45	92	29	1	58	74	79
October	2	2	0	0	202	238	24
November	10	0	0	0	23	61	8
1959							
January	22	0	0	0	86	32	7
February	12	0	3	0	107	40	24
April	140	0	1	0	99	131	0
May	114	73	10	0	81	622	228
June	4	99	2	0	52	3	9
August	0	0	12	0	96	36	7
September	0	0	0	0	0	0	0
December	0	0	0	0	0	0	0
1960 [e]							
May	8	0	0	0	11	0	0

[a] Collecting-sites are numbered from upstream down separately for each branch canal; thus collecting-site 5 (in the north canal) should not be taken to be downstream of collecting-site 4 (in the south canal).
[b] Predominantly *Tropicorbis* at these sites.
[c] Predominantly *Australorbis* at these sites.
[d] A dash indicates that no collection was made.
[e] The snail population was sparse throughout 1960.

with interruption of flow, since, as mentioned above, the flow was maintained almost continuously. Periodic removal of vegetation, usually at 3-month intervals, was probably critical (Pimentel & White, 1959b), but our observations showed that snails persisted in considerable numbers in spite of this event. Certainly annual population peaks and complete disappearances were not attributable to canal cleaning. The disappearance of *Australorbis* at site 4 (south) was linked with a persistent heavy deposit of silt in front of a siphon taking the water under a road. The *Tropicorbis* colony at site 6 (north), which was more persistent than others, was located at a 100-yard (90-m), right-angle bend in the canal.

In sum, instability in the snail population of Guajataca canal occurred in spite of uninterrupted water flow, implying unrecognized factors.

Juana Diaz irrigation system

The Juana Diaz irrigation system serves a sugarcane area in south-central Puerto Rico with water from Lakes Coamo and Guayabal; planorbid snails occur in the latter. The upper portions are cement-lined, and flow is rapid; such sections were abandoned when snails were not collected in initial surveys Three collecting-sites in mud-lined terminal sections were selected for observations. Only *Tropicorbis riisei* was ever found. It occurred in abundance infrequently, fluctuated with sporadic propagation and maximum numbers of snails did not persist until the following survey (Table 7).

TABLE 7
SUMMARY OF PERIODIC COLLECTIONS OF *TROPICORBIS RIISEI* IN JUANA DIAZ IRRIGATION CANAL

Month of collection	No. snails per 25 dips at collecting-site:		
	1	2	3
1957			
October	42	23	107
December	4	0	75
1958			
January	126	61	Canal dry
March	36	19	8
April	5	17	13
June	8	14	5
July	106	21	8
September	8	33	7
October	27	1	0
December	0	0	0
1959			
January	41	47	2
March	28	17	0
April	16	3	1
July	6	50	0
1960			
May	0	0	0

Annual peaks were not evident, as they had been in the Guajataca canals. There was no apparent explanation for the absence of *Australorbis* since it has been collected in one of the source lakes and occurs in surrounding areas. During 1959, *Tarebia* appeared in the canal and quickly populated in great numbers. It is also present in the source lakes.

Patillas irrigation system

The Patillas irrigation system includes Lake Patillas and serves sugar-cane fields along a 25-mile (40-km) canal in south-central Puerto Rico. The canal is lined with soil; the water flow is medium; and vegetation is commonly dense, requiring manual removal once or twice a year. The flow-rate varies greatly, and flow is frequently stopped when irrigation demands are low. Six permanent collecting-sites were established throughout the length of the canal in April 1957 (Table 8). Both *Australorbis* and *Tropicorbis* were present, but only the latter normally occurred in the lower half of the canal, while *Australorbis* was dominant in the upper half. *Australorbis* was initially very abundant, with extremes of 2000 snails in 25 dips at certain of the upper collecting-sites. In June 1957, snails were destroyed upstream to the point of near-eradication, coincident with termination of flow. For almost a year snails were sparse in spite of one or two abortive periods of propagation. Fluctuations in populations continued at a low level throughout 1959. In May 1960, a dominance of *Tropicorbis* was noted in the upper sections of the canal, but a dense colony of *Australorbis* did prevail at the third site downstream. Infected snails have been collected in the main waterway (site 3).

The Patillas canal was the most prolific of the several systems studied, as indicated by the enormous snail population from April to June 1957. At this time, occurrence of near-eradication was certainly linked with termination of flow for two periods of four days. The reason for complete absence of repopulation during 1957-58 is uncertain, and this occurrence is in contrast to the moderate propagation during the remainder of 1958 and 1959. Such inconsistencies may be due to irregular interruptions of flow, determined by irrigation demands. The concentration of snails in Patillas canal has been deemed critical in the repopulation of natural streams following chemical control and prolonged, severe, dry seasons.

Lago Dos Bocas

A study of Lago Dos Bocas was begun in June 1958. The lake has three tributaries, two of which were observed. *Australorbis* was found in the

TABLE 8
SUMMARY OF PERIODIC COLLECTIONS OF *AUSTRALORBIS* AND *TROPICORBIS* IN PATILLAS IRRIGATION CANAL

Month of collection	No. snails per 25 dips at collecting-site:					
	1	2	3	4	5[a]	6[a]
1957						
April	958	930	117	11	102	3
May	1 374	904	331	51	69	3
June	1 849	2 037	477	49	71	11
June	1	0	0	14	11	7
July	2	0	1	0	6	3
August	0	0	0	1	10	1
September	1	0	0	0	3	2
October	0	0	0	1	7	43
November	0	0	1	0	0	89
1958						
January	0	1	1	0	1	15
February	0	0	1	0	0	1
March	0	0	0	0	0	2
June	0	0	30	39	9	4
July	31	27	14	31	49	7
September	74	59	1	2	1	3
October	501	280	9	34	16	Canal dry
November	261	219	6	4	13	0
December	267	34	0	20	Canal dry	Canal dry
1959						
January	1	6	6	16	0	6
March	5	15	34	13	0	18
April	1	2	1	20	—[b]	5
July	2	0	0	0	0	45
1960						
May	449[a]	244[a]	411[c]	0	0	0

[a] Predominantly *Tropicorbis*.
[b] No collection made.
[c] Mixed *Australorbis* and *Tropicorbis*.

eastern tributary at the point where flow is reduced as it becomes confluent with the lake proper. At collecting-site 1, farthest upstream, snails were abundant in March 1958, prior to the beginning of the periodic surveys, but at no time during two years of observation were such numbers again present, and they remained negligible at four collecting-sites (Table 9). Apparently, it is a rare occurrence to find snails in this habitat. The few snails obtained were at the edge of the water in the river-lake junction. No snails were found in this location in the western tributary, but they did occur regularly in sparse numbers in a marginal swamp (collecting-site 5), disjunct from the channel except at times of high waters. Marginal pools up-river in the western tributary contained *Australorbis*, constituting a source of human infection at Utuado. Several surveys of the lake margin and of the extensive masses of floating *Piaropus* during the study period did not reveal the vector snail, but *Tarebia* was present in enormous numbers. The hazard of human exposure to bilharziasis in Lake Dos Bocas, for instance, through fishing and related activities, was negligible during the period of our observations.

TABLE 9
SUMMARY OF PERIODIC COLLECTIONS OF *AUSTRALORBIS* IN LAGO DOS BOCAS

Month of collection	No. snails per 25 dips						
	Eastern tributary collecting-sites:				Western tributary collecting-sites:		
	1 [a]	2	3	4	5 [b]	6	7
1958							
June	0	1	1	0	—[c]	0	0
August	2	0	0	0	—	0	0
September	1	0	0	0	26	0	1
October	11	1	1	0	24	0	0
December	2	—	0	2	10	0	0
1959							
March	16	0	0	0	8	0	0
May	3	0	0	0	14	0	0
August	3	0	0	0	4	2	0
November	2	0	—	1	12	0	0
1960							
February	0	—	—	0	25	0	0
July	6	4	—	0	6	0	0

[a] Initial collection in March 1958 revealed more than 20 snails per square yard.
[b] Marginal swamp.
[c] A dash indicates that no collection was made.

Farm ponds

Farm pond surveys near Salinas and Peñuelas in southern Puerto Rico revealed only *Tropicorbis* in five ponds. *Australorbis* occurred in one (pond 5) initially, but was finally replaced by *Tropicorbis* after the pond had been cleaned with bulldozers. The snails were sparse with few exceptions, and, when numerous, they did not persist until the following survey. Marked fluctuations of water level in these ponds tend to make them unfavourable for planorbids, but explosive propagation does occur occasionally, as indicated by massive numbers of shells along the banks.

DISCUSSION

This study had a single primary objective—the determination of population density patterns of *Australorbis* during a sequence of propagative periods—which was achieved by periodic observation made at permanent collecting-sites in a variety of habitats over a period of two or more years.

Quantitation of snail densities on the basis of an arbitrary number of dips with a standard scooping procedure [1] was judged the most suitable because of the limited size of the collecting-sites, the limited time that could be given to each, and general field conditions. This decision was based on an initial comparison of snail collecting methods [2] (Olivier & Schneidermann, 1956; Hairston et al., 1958).

The use of a six-week collecting interval appeared to be favourable for detecting population changes. Disappearance of a colony and repopulation within this interval was essentially precluded on the basis of laboratory data (Hernandez & Ritchie, 1958). To determine snail growth in field populations would probably require weekly collections, as

[1] Gerhardt, C. E. (1956) Unpublished summary of investigations No. 7, Technology Branch, Communicable Disease Center, Public Health Service, US Department of Health, Education, and Welfare.

[2] Annual reports of the 406th US Army Medical General Laboratory for the years 1952 and 1954 (unpublished).

TABLE 10
SUMMARY OF PERIODIC COLLECTIONS OF *AUSTRALORBIS* AND *TROPICORBIS* IN FARM PONDS [a]

Month of collection	No. snails per 25 dips in pond:					
	1	2	3	4	5 [a]	6
1958						
March	0	11	5	35	51	—[b]
July	9	9	11	12	94	21
September	1	30	0	18	19	274
October	0	6	3	0	25	11
December [c]	0	0	0	0	0	0
1959						
January	—	6	0	8	222	44
March	11	3	12	—	24	28
April	7	15	14[d]	4	10	41
July	0	3[e]	7[e]	17	3	20

[a] All ponds had only *Tropicorbis* except pond 5, in which an initial population of *Australorbis* was replaced by *Tropicorbis* after December 1958.

[b] A dash indicates that no collection was made.

[c] In this month three ponds were drained and sprayed with herbicides and the others were dried or cleaned.

[d] *Heliosoma* and *Tarebia* found, but not counted.

[e] *Marisa* found, but not counted.

indicated by field growth-rates reported by Olivier & Barbosa (1955).

A marked predominance of *Tropicorbis* was observed in four of five main irrigation systems in Puerto Rico and in six farm ponds in the southern part. It was the only planorbid collected in two of the main irrigation canals and was dominant at certain places in the other two. Both *Tropicorbis* and *Australorbis* are limited chiefly to the primary irrigation canals, being of little concern in the secondary and tertiary channels and within the cane fields, because of frequent drying. In the lake-reservoirs of four systems, planorbids are present; but they rarely, if ever, exceed a sparse density.

Among 50 collecting-sites in several kinds of habitat, periodically observed for about two years, a truly stable population of neither *Tropicorbis* nor *Australorbis* was encountered, i.e., a population in which mixed sizes regularly occurred and which displayed the quality of persistence. Dense populations seldom persisted for more than a few months. Periods with negligible propagation often persisted for months or over a year, snail populations reaching low densities until they were sometimes uncollectable. Existence for the individual planorbid is hazardous and a brief egg-to-egg cycle (Olivier & Barbosa, 1955; L. S. Ritchie, L. Berrios-Duran & R. Deweese [1]) appears critical in species survival. Continuous or seasonal propagation was not evident; and if a propagative pattern exists in Puerto Rico, it is not well defined generally, and within separate habitats would appear to be only sporadically dynamic. As was also reported by Olivier & Barbosa (1955) and Liétar (1956), we frequently found eggs of *Australorbis* without subsequent evidence of propagation, and dense mature colonies sometimes showed little evidence of egg-laying. Such situations should be investigated as examples of exigencies imposed by nature which might be experimentally induced for snail control or to enhance the effectiveness of chemical control. Planned interruptions of flow (including drying) in irrigation canals might be quite effective in suppressing planorbid snails.

Important correlations may exist between the marked fluctuations and instability of *Australorbis* in Puerto Rico, and the epidemiology of bilharziasis. For example, the *Australorbis* population of the hyperendemic Barranquitas Valley was studied in detail in 1953 and it was found that these snails were abundant and widely distributed in the generally high-gradient stream system. A gross check was made annually and declines were evident. In 1956-58 a careful survey, made by W. B. Rowan, covered every water body in the well-limited catchment-area and no *Australorbis* were observed. Snails reappeared during the first part of 1960 and became numerous during 1961. The assumed absence may possibly be correlated with a marked decline (50%) in human bilharziasis incidence observed in all age-groups during the period 1953-55 by Maldonado & Oliver-Gonzalez (1958). Exposures under conditions described in this paper would tend to be sporadic rather than continuous, thus possibly allowing for acquisition of resistance from single or short series of multiple exposures.

The occurrence of stringent natural control of *Australorbis* in Puerto Rico, sometimes accounting for near-eradication, is indicated by our investigations. The factors involved are poorly understood, but it is known that floods sometimes wash out snails from streams and rivers (Pimentel & White, 1959a; Rowan, 1959). Also, the presence of eggs in a habitat without subsequent appearance of juvenile

[1] Unpublished manuscript.

snails has been observed by Olivier & Barbosa (1955), by Liétar (1956) and in the current study. These and other less-known influences imposing natural control must be clarified and exploited, if possible, to enhance the effectiveness of molluscicides and other control measures. The proper timing, frequency and concentration of molluscicidal applications for periods of low and high snail propagation should be investigated in relation both to destruction of mature populations and to repopulation control by repeated, frequent applications.

Frequent and prolonged depressions in *Australorbis* populations could lead to false conclusions regarding the benefits of snail control measures, particularly in relation to repopulation. If the Aibonito stream, for instance, had been treated with molluscicides at the end of 1958, just prior to the 18-month period of very low propagation, a biased conclusion regarding repopulation might have resulted. This would be particularly unfortunate in field-testing potential molluscicides. Moreover, misevaluations of control measures other than the use of molluscicides might also result, particularly when snail populations are naturally suppressed for several years, as occurred in the Caguitas and Barranquitas valleys.

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RÉSUMÉ

A Porto Rico, l'évolution naturelle des populations d'*Australorbis glabratus* a été étudiée pendant plus de deux années au cours desquelles les mollusques étaient capturés à intervalles de six semaines, selon une technique standardisée, en 50 sites de récolte représentatifs des divers types d'habitats rencontrés dans la région. Dans quatre réseaux d'irrigation sur cinq, *Tropicorbis* prédomine et vit à l'instar de *A. glabratus* dans les canaux de distribution principaux où il ne risque pas d'être détruit par la mise à sec qui serait éventuellement un moyen de lutte à utiliser. Ni l'une ni l'autre de ces espèces ne se présente sous la forme de populations stables à l'intérieur desquelles on observerait une croissance saisonnière ou progressive. Leurs colonies ne présentent jamais de densité élevée pendant plus de quelques mois: sous l'effet de causes indéterminées, elles sont des mois, voire plus d'une année, sans se reproduire; les mollusques vecteurs sont alors à ce point décimés qu'ils ne figurent plus dans les prélèvements. Ces faits méritent d'être mieux connus, car il existe une corrélation prouvée entre la présence des mollusques et l'incidence de la bilharziose: à partir de 1953, les populations d'*Australorbis* ont décliné pour disparaître complètement en 1956-58, et réapparaître en 1960 — alors que de 1953 à 1955 la bilharziose a diminué de 50%. Etudier l'histoire naturelle de cet agent vecteur serait du plus grand intérêt si l'on veut coordonner efficacement la mise en œuvre des molluscicides avec la régression spontanée de ses populations. Eventuellement, cela permettrait aussi de mieux évaluer l'action des produits utilisés. Les données épidémiologiques régionales de la bilharziose devront être chaque fois relevées avec le plus grand soin.

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